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Research Article

# Effects of management complexity on the composition, plant functional dominance relationships and physiognomy of high nature value grasslands

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## Abstract

A significant proportion of Europe's species-rich grasslands are semi-natural habitats. They have a long history of traditional management. Several studies have been carried out to conserve them, resulting in the establishment of subsidised conservation management schemes. On the other hand, many of these conservation management schemes have failed to provide locally adaptive solutions to maintain the diversity and functional status of species-rich grasslands. In addition, few studies have compared the conservation effectiveness of different levels of management complexity. The levels of management complexity in our study are based on how different management types (e.g. grazing and mowing etc.) and how different herbage removal intensities (e.g. lower and higher grazing intensities) are combined within and between years. To investigate this, we compared the overall effects of management complexity, herbage removal intensity and management type on plant diversity, plant functional type dominance relationships and plant physiognomy. Our field sampling was carried out in the sandy meso-xeric grasslands of the Turján Region of the Great Hungarian Plain (Central Hungary). We sampled nine 2 m × 2 m plots per grassland site (n = 12), recorded all the rooted plant species and estimated their percentage cover in each plot. High level of management complexity had significant positive effects on plant diversity, grazing had positive effects on plant diversity and phanerophyte density, while the studied levels of herbage removal intensity had no effect on diversity, plant functional types or plant physiognomy. In parallel, mowing and/or low levels of management complexity had some negative effects on conservation value (e.g. lower Shannon and Simpson diversity). In this landscape, the dominance of grazing and the more complex management is more optimal

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than relatively homogeneous mechanical mowing. The choice of management type and intensity is an important tool in the conservation management system of this landscape, but so too is its appropriate application in space and time. Through a detailed analysis of the effects of management complexity levels compared to management types and herbage removal intensity levels, we provide a new opportunity to make grassland management practices more effective for conserving biodiversity in this region, but it would be important to investigate these in different landscapes and conditions.

**Key words:** Grassland conservation system, management effects, management efficiency

## Introduction

A significant proportion of European landscapes are cultural landscapes that have been transformed and managed by humans (Plieninger et al. 2006; Dahlström et al. 2013). The majority of the grasslands in these landscapes are semi-natural, i.e. created and actively maintained by local communities (Maurer et al. 2006; Marini et al. 2007; Niedrist et al. 2009). Nevertheless, the number of endemic species in these grasslands is exceptionally high in Europe, underlining their high conservation value (Hobohm and Bruchmann 2009; Habel et al. 2013).

Species-rich, semi-natural grasslands have been managed for centuries by small family farms to provide summer forage in pastures and to produce winter fodder in hay meadows for livestock (Babai and Molnár 2014). Economic, socio-cultural and political factors, such as intensification and abandonment, have led to the disappearance of extensive grassland management systems across Europe since the mid-twentieth century (Bakker and Berendse 1999; MacDonald et al. 2000; Öckinger et al. 2006). As a result, the habitat mosaic of the cultural landscapes has changed, with fragmentation and disappearance (scrub encroachment, afforestation) of species-rich semi-natural grasslands having occurred, while the biodiversity of these habitats has declined (Eriksson et al. 2002; Krauss et al. 2004; Öckinger and Smith 2006; Flynn et al. 2009; Laliberte et al. 2010).

As semi-natural grasslands have been developed and maintained by human management, active and adaptive nature conservation management should be implemented to maintain the species composition and vegetation structure of these habitats. Through a long learning process, nature conservation aimed to mimic the patterns and disturbance regimes of former non-intensive, traditional grassland management (Szépligeti et al. 2018; Kun et al. 2021). These principles recognise the importance of the co-formation of the vegetation and extensive management and the adapted nature of the species pool to the former management practices (Poschlod et al. 1998).

Conservation management of grasslands should also draw on the experience of local communities still practising traditional and adaptive grassland management (cf. Niedrist et al. (2009); von Glasenapp and Thornton (2011)), as in the case of experiments in conservation biology (e.g. Vadász et al. (2016)). One of the most significant trends in conservation management research is the oversimplified 'one-factor' view, where ecologists study the effects of only one management factor, mostly focusing on the general effects of management type (mostly grazing and/or mowing) and management intensity (Tälle et al. 2016;

Török et al. 2018; Kun et al. 2021). The explanatory power of these specialised and generic few-factor models often has major limitations in their applicability to specific and local grassland conservation practices (Vadász et al. 2016; Kun et al. 2019). Therefore, more effective and practice-orientated nature conservation also requires more detailed and comprehensive studies to fill the knowledge gaps on the complex, locally specific effects of different management factors (e.g. locally appropriate management types, regimes, spatial and temporal applications etc.) on species-rich grasslands (Babai et al. 2015; Kun et al. 2021). One of the potentially important management factors for grassland conservation that should be investigated is how different management factors are applied spatially and/or temporally on grasslands (Allan et al. 2014). Based on some previous studies (Vadász et al. 2016; Kun et al. 2019), the spatial and temporal application of management types (e.g. grazing or mowing) or different herbage removal intensities (temporal speed of grazing or mowing, based on standard livestock unit and mowing frequency, see Table 1) can represent management complexity. Levels of management complexity are based on how different management types (e.g. grazing or mowing) and different management intensities are varied within and between years on a given grassland (see Table 1 for details). With more knowledge about the appropriate application of levels of management complexity, we would be able to more effectively adapt our conservation objectives in different grassland conservation management cases (Kun et al. 2019).

In this study, we aim to reveal the effects of management complexity, management intensity levels and management types on plant diversity, plant functional type dominance relationships and plant physiognomy in species-rich meso-xeric, sandy grasslands of central Hungary. We hypothesise that high management complexity and low herbage removal intensity will positively affect plant diversity, plant functional state and physiognomy. We also hypothesise that grazing, in particular, has a positive effect on higher plant diversity and less graminoid (Poales) cover, more forbs and shrubs (Phanerophytes) cover. Our specific question is: How do low and high levels of management complexity affect plant diversity, vegetation physiognomy and plant functional type cover in relation to management type and herbage removal intensity?

**Table 1.** A list and an introduction to the management factors and their categories and sub-categories.

| Management factor categories | Management factor subcategories |
|---|---|
| **Type of grassland management (*T*)** | **Mowing (*M*):** Mechanical mowing at the end of June or the first half of July with 10–15 cm of stubble. See details of management complexity later in this Table. |
| | **Grazing (*G*):** Pastures are mainly grazed by cattle from the end of April to the beginning of October each year. Shepherds often work with them. |
| | **Combined (*C*):** Mowing and grazing are combined within the same year or between years. For more details, see management complexity later in this Table. |
| **Herbage removal intensity (*I*)** | **Low:** Grazing at < 0.5 Standard Livestock Units (SLU) per hectare or mown once a year. LUI value: 0.1 (Schneiders et al. 2011). |
| | **High:** Grazing at > 0.5 Standard Livestock Units (SLU) per hectare or mown once a year followed by grazing in the same year. LUI value: 0.2 (Schneiders et al. 2011). |
| **Management complexity (*C*)** | **Low:** Grazing with a standard sequence of two grazing units per year or one mowing with 10% uncut per year or one mowing per year combined with subsequent grazing. |
| | **High:** Mowing and grazing combined between years or grazing with different start times between years in a four-year rotation. |

# Methods

## Study area

The study sites are located in the Turján Region of the Great Hungarian Plain along the Danube in central Hungary, in the northern Kiskunság area. The study sites are relatively close to each other, within a circle of about 10 km diameter around the neighbouring villages of Kunpeszér, Tatársszentgyörgy and Kunadacs (Appendix 1). The climate is mainly continental with sub-Mediterranean influences. The average annual temperature is 10.5–11 °C, while the average annual precipitation is 500–550 mm (Kocsis 2018). The potential natural vegetation is the Euro-Siberian steppic woods with *Quercus* spp. A significant part of the region consists of semi-natural *Molinia* meadows, which are mown or grazed by cattle and Pannonic sand steppes. These grasslands are mainly grazed by Hungarian Grey cattle and Charolais breeds and, to a lesser extent, by sheep.

Most of the studied sites have been modified by local people in the past and present, through woodcutting and long-term grazing (Molnár et al. 2022). Some of the grasslands studied are old fields, abandoned several decades to a few centuries ago. These areas are fully regenerated and are well developed. Their species pool, species composition and physiognomy do not differ significantly from the other grasslands studied. Constant management is essential in these grasslands to prevent reforestation and the spread of some native disturbance-tolerant or invasive alien species (Erdélyi et al. 2023). Over the past century, a network of drainage canals has been constructed throughout the area, resulting in the drying out of wet grasslands and the creation of a significant amount of drier grassland (Tölgyesi et al. 2022). All of the grasslands studied are meso-xeric habitats, representing the transitional zone between the *Molinia* meadows (*Molinion caeruleae*) and the dry Pannonic sand steppes (*Festucion vaginatae*), with a similar vegetation composition and state of development. This species-rich grassland covers a large area in the study area; but it is threatened in a regional and wider context. The meso-xeric grassland habitats are important for the whole Eurasian forest-steppe zone and can be considered as its species-rich grassland component (Mathar et al. 2016; Willner et al. 2019). The dominant and characteristic graminoid (*Poales*) species of the studied grasslands include *Chrysopogon gryllus*, *Brachypodium pinnatum* and *Molinia caerulea* and some forb species, such as *Serratula tinctoria*, *Sanguisorba officinalis*, *Peucedanum cervaria*, *Betonica officinalis* and *Genista tinctoria*, as well as some Hungarian protected forb species, such as *Ophrys sphegodes*, *Iris spuria*, *Centaurea scabiosa* subsp. *sadleriana* etc. All the grasslands studied are part of the Kiskunság National Park. As a result, these grasslands have been managed according to conservation principles in the last decades which means a lower management intensity and a more complex management in space and time in general. Conservation is carried out throughout the study area by the Kiskunság National Park Directorate.

## Data collection

The surveys were conducted in June 2018 on 12 grassland sample sites, all of which were at least 5 ha and at most 10 ha in size (Appendix 1). Three of the sites were mown, six were pastures with varying levels of herbage removal intensity and complexity and, in three grasslands, these had combined use

(both mowing and grazing). For each study site, nine plots (2 m × 2 m each) were located in the inner zone of the grassland to exclude edge effects. In each grassland, a random starting point was chosen and the plots were sampled along two parallel line transects with a maximum length of 200 m and a minimum distance of 4 m between plots (Appendix 2).

The coordinates of the plots were recorded by GPS. Data were collected from 108 plots in the 12 grassland sites mentioned above, nine plots per site (see Appendices 1 and 2). During sampling, we recorded each vascular plant species found in the sample plots and visually estimated its percentage cover. In addition, we visually estimated four vegetation physiognomic characteristics: 1) percent litter cover, 2) total plant cover, 3) the amount of bare soil surface and 4) average plant height. Average plant height was estimated using a tape measure and reported in centimetres. Due to overlapping layers of vegetation, total plant cover in plots could exceed 100%.

We defined plant functional types (PFTs) as groups of species based on three growth forms: *forbs* including non-grassy herbs, graminoids (*Poales*) including grasses, sedges and rushes and *phanerophytes* including shrubs and small trees (Raunkiær 1934; Box 1996; Király 2009). We calculated the proportions of PFTs in each plot by summing the cover values of the species assigned to them.

At each grassland site, we recorded three management factors at different levels, including intensity of herbage removal (***I***, with low and high levels), complexity of management (***C***, with low and high levels) and different types of management (***T***, including grazing, mowing and combined types) (Table 1). Prior to our field sampling, we interviewed the conservation practitioners of the later sampled grasslands of the National Park Directorate and sampled grassland sites were selected, based on low and high levels of complexity and herbage removal intensity of management, as well as management types (grazing, mowing or combined). On each of the sampled grassland sites (n = 12), all three management factor categories (***T***, ***I***, ***C***) were applied, but only one subcategory of each management factor category was applied, for example, on a grazed site (one management type), only low or only high level of herbage removal intensity and only low or only high level of management complexity were applied (see Appendix 3). These management techniques on grasslands have been stable in the last decades and were only started by the Kiskunság National Park Directorate in the Turján Region (see Vadász et al. (2016)).

## Data analysis

We calculated diversity measures, namely species number, Shannon index and Simpson index, from the plant species and estimated percent cover data recorded in each plot. The use of both diversity indices was important because the Shannon diversity index is more sensitive to the higher proportion of rare (often specialist) species, while the Simpson index is more sensitive to the balance of more dominant species. We built linear and generalised linear mixed effects models (with 'lmer' and 'glmer' functions from the 'lme4' package) to test the effect of management factors ***T***, ***I*** and ***C*** as three fixed factors on plant diversity indices, on the abundance of PFTs and on vegetation physiognomy. Different families of distributions (Gaussian and Gamma) were used to treat each differently distributed dependent variable in the modelling (the 'gamma_

test' function from the 'goft' package was used). In our analyses, site was a random factor in all models. To assess model fit, marginal $R^2_{LR}$ was applied (Ives 2019) from the 'MuMIn' package in R 3.5.1. The beta $R^2_{LR}$ statistic (Edwards et al. 2008) was applied using the 'r.squaredLR' function to assess the best-fitting model amongst those run with each factor (*T*, *I* and *C*) separately as a predictor. The levels of the fixed factors ***T***, ***I*** and ***C*** were compared using the LMER Tukey post hoc test with the Bonferroni adjustment method (Hothorn et al. 2009) from the 'multcomp' package and with the 'glht' function. PERMANOVA analysis (with the 'adonis' function from the 'vegan' package) was used to investigate general patterns in species composition via possible effects of management factors. Principal component analysis (PCA) (using the 'pca' function from the 'vegan' package) was used to investigate the relationships between plant diversity, plant functional types and physiognomic factors in relation to different management factors. Our analyses were performed in the R 3.5.1 (R Core Team 2018) software environment (R Core Team 2018).

## Results

Management type, levels of herbage removal intensity and management complexity had similarly strong effects on species number based on model fits ($R^2$ > 0.320, Table 2). There were no differences between low and high levels of herbage removal intensity for diversity, plant functional types and physiognomic factors. High levels of management complexity resulted in significantly higher Shannon and Simpson diversity (Fig. 1). In the case of ***T***, grazing and combined management resulted in significantly higher Shannon and Simpson diversity than mowing and grazing had significantly higher phanerophyte cover than mowing, but no significant difference in species number was observed (Appendix 4).

With PFT categories as dependent variables, management type showed a strong relationship with graminoid and forb cover (Table 3). Grazed sites had a significantly higher proportion of phanerophyte cover than mown sites and combined sites were between the two (Appendix 4). Herbage removal intensity showed a strong relationship with forb and graminoid cover, but a weaker

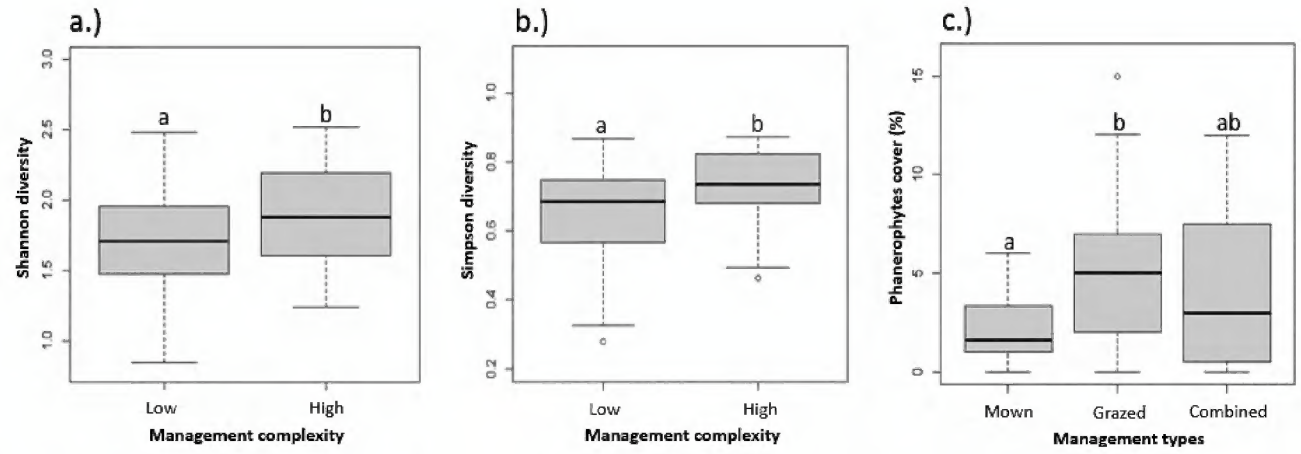


**Figure 1.** Significant differences in diversity and cover of phanerophytes in grasslands with low and high management complexity and different management types. Only models with minimum $R^2_{LR} \geq 0.100$ fit (see Tables 2–4) and significant differences (Appendices 4–6) were selected for inclusion. Significance of differences between groups is based on the LMER Tukey post hoc tests. Significant differences ($p < 0.05$) between factor levels are indicated by letters ('a' and 'b') above the boxplots. Non-significant differences are indicated by the letters 'ab'.

relationship with phanerophyte cover (Table 3). There were no significant differences between the levels of herbage removal intensity (Appendix 5). ***C*** had a stronger relationship with the forbs and graminoid groups, but a weaker relationship with the phanerophyte group (Table 3). Apart from these relationships, no significant differences were found between ***C*** levels for PFTs (Appendix 6). ***T***, ***I*** and ***C*** strongly influenced average plant height, litter cover and total plant cover, in general (Table 4). On the other hand, no significant differences in average plant height, litter cover and total plant cover were observed between grasslands exposed to different levels of ***T***, ***I*** and ***C*** (Appendices 4–6).

The two main components were presented in relation to forbs and graminoid (Poales) cover, based on principal component analysis. Higher graminoid cover was associated with mowing and higher forbs cover was mostly associated with grazing and combined management was intermediate between mowing and grazing (Fig. 2). High herbage-removal intensity was associated with higher graminoid cover and low herbage-removal intensity was associated with higher forbs cover (Fig. 3). A high level of management complexity was associated with higher forbs cover and a low level of management complexity was asso-

**Table 2.** Effects of different management factors, namely ***T*****:** management type; ***I*****:** herbage removal intensity of management; ***C*****:** management complexity, on diversity measures in terms of model fit. Goodness-of-fit is expressed as $R^2_{LR}$ values.

| Management factors | Species number | Shannon diversity | Simpson diversity |
|---|---|---|---|
| | $R^2$ | $R^2$ | $R^2$ |
| *T* | 0.324 | 0.096 | 0.057 |
| *I* | 0.325 | 0.023 | 0.011 |
| *C* | 0.324 | 0.072 | 0.053 |

**Table 3.** Effects of different management factors, namely ***T*****:** management type; ***I*****:** herbage removal intensity of management; ***C*****:** management complexity in relation to forbs, graminoid and Phanerophyte cover. Goodness-of-fit is also presented in $R^2_{LR}$ values.

| Management factors | Forb species cover (%) | Graminoid species cover (%) | Phanerophyte species cover (%) |
|---|---|---|---|
| | $R^2$ | $R^2$ | $R^2$ |
| *T* | 0.368 | 0.430 | 0.121 |
| *I* | 0.365 | 0.420 | 0.075 |
| *C* | 0.368 | 0.415 | 0.097 |

**Table 4.** Effects of different management factors, namely ***T*****:** management type; ***I*****:** herbage removal intensity of management; ***C*****:** management complexity in relation to physiognomic factors in relation to grasslands. Goodness-of-fit is also presented in $R^2_{LR}$ values.

| Management factors | Litter cover (%) | Total plant cover (%) | Bare soil surface (%) | Average plant height in plots (cm) |
|---|---|---|---|---|
| | $R^2$ | $R^2$ | $R^2$ | $R^2$ |
| *T* | 0.579 | 0.709 | 0.120 | 0.355 |
| *I* | 0.572 | 0.705 | 0.090 | 0.298 |
| *C* | 0.559 | 0.703 | 0.115 | 0.318 |

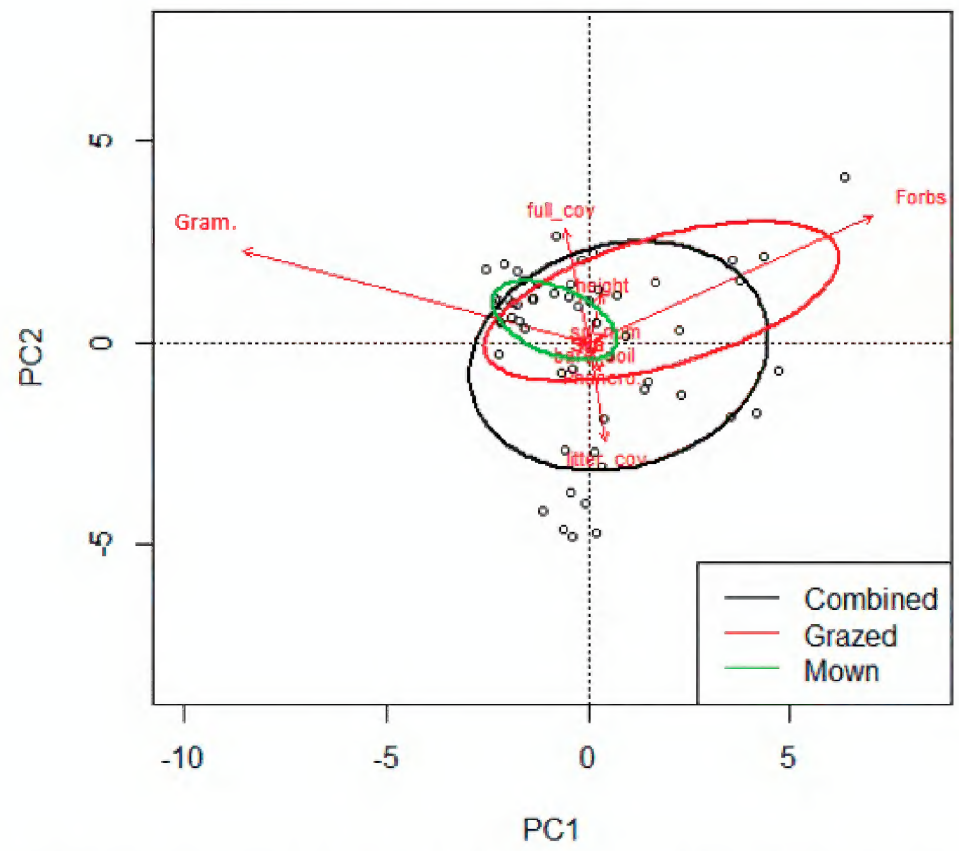


**Figure 2.** Principal Component Analysis of diversity indices, plant functional type cover and physiognomic factors across management types. The diversity indices examined are species number (sp_num), Shannon (Sha) and Simpson (Sim) diversity. Plant functional type cover includes graminoids (Gram.), forbs and phanerophytes (Phanero.). Plant physiognomic factors are average plant height (height), total plant cover (full_cov), bare soil surface (bare_soil) and litter cover (litter_cov). Management types: mown, grazed and combined management. The direction, width and different colours of the ellipses in the figure show us the relationship between the samples of different management types. The length and direction of the arrows show the explanatory power and relationship of each variable studied with management types and other variables.

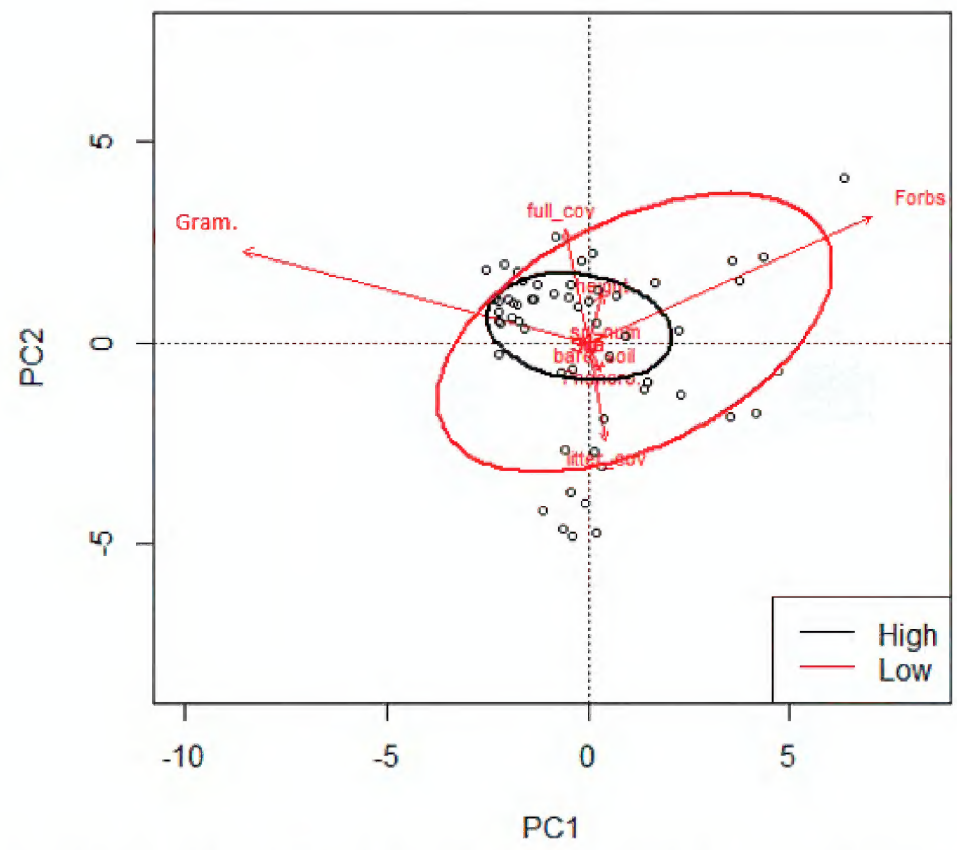


**Figure 3.** Principal Component Analysis of diversity indices, plant functional type cover and physiognomic factors across herbage removal intensity levels. The meaning of the abbreviations used in this Figure is given in the legend to Fig. 2.

ciated with higher graminoid cover (Fig. 4). Further details on the importance of the principal components, based on the proportion of variance explained by them, can be found in Appendix 8.

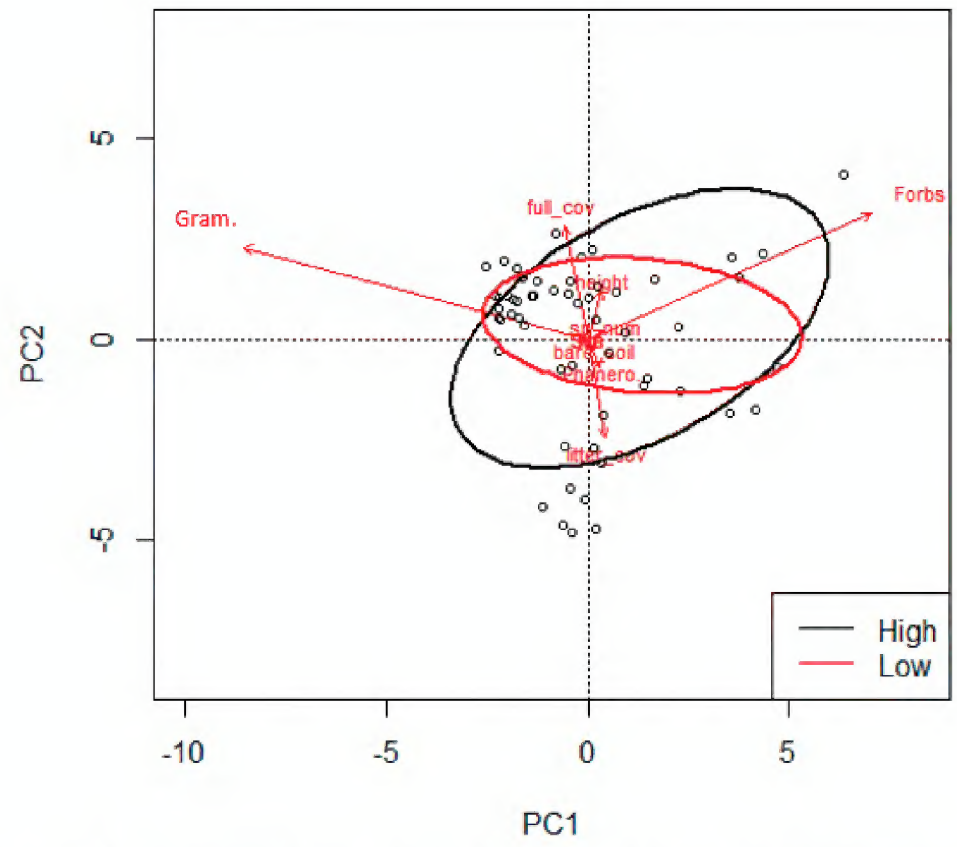


**Figure 4.** Principal Component Analysis of diversity indices, plant functional type cover and physiognomic factors across management complexity levels. The meaning of the abbreviations used in this Figure is given in the legend to Fig. 2.

## Discussion

### Effects of different management, plant functional type cover and physiognomic factors on grassland diversity

Different management types, mainly mowing and low and high levels of herbage removal intensity and management complexity, significantly affected the species composition and dissimilarity ratios of the grasslands studied (Fig. 1, Appendix 7). In addition, we found a strong positive effect of high management complexity (***C***) on species number and, to a lesser extent, on Shannon and Simpson diversity and forbs and a negative effect on predominantly perennial and clonal graminoids (Figs 1, 4). The ***C*** increases when different management types (***T***) and herbage removal intensities (***I***) are varied in space and time (see Table 1; Vadász et al. (2016)). Certain species or groups of species are likely to prefer certain combinations of ***T*** and ***I***, while they may become locally extinct if other combinations are practised for a long time. When ***C*** is high, many combinations of ***T*** and ***I*** occur at least once within a time-frame of a few years, providing opportunities for most species to experience a favourable year, preventing extinction (Catorci et al. 2014; Kun et al. 2021). For physiognomic factors (e.g. litter cover and average plant height), ***C*** levels did not play a significant role and these variables are better determined by the type of management.

Although different ***T*** choices played a less important role in influencing compositional diversity, the choice of the appropriate management type was also significant: grazing had a more positive effect on phanerophytes than mowing (Appendix 4). This difference can be explained by the most extensive, professional cattle grazing on the studied grasslands and by the selective and structuring grazing behaviour of cattle (i.e. cattle avoid shrubs etc.) and/or other grazers (Dumont et al. 2012; Molnár et al. 2020). The presence of phanerophyte species and their adequate control by grazing can lead to greater structural or physiognomic heterogeneity of grasslands. The effect of grazing is in contrast

to that of mowing machines, which cut all plants uniformly in mid-summer with a low stubble height. As a result, mown sites could become more homogeneous in vegetation structure. By creating microhabitats and increasing structural variability by allowing a greater cover of phanerophyte species (mostly native shrubs, such as *Crataegus monogyna*, *Prunus spinosa* etc.), extensive grazing can contribute to the generative reproduction of herbaceous plants in grasslands (Kelemen et al. 2017). Furthermore, the application of grazing, mowing or a combination of both also resulted in slight differences in Jaccard-based species composition (but not low or high ***I*** and ***C*** levels) (Appendix 7). We argue that these phenomena may positively influence species richness. The nurturing effect of shrub species may help the generative and vegetative reproduction of grassland species in the actively managed natural and semi-natural grassland communities in the forest-steppe zone (Kelemen et al. 2017). On the other hand, it is fundamental to keep the phanerophyte cover within an optimal range (~ 1–10%), which prevents reforestation. An extensive grazing regime can be an efficient way to optimally control the number of shrubs on grasslands. Like shrubs, many forbs can be considered important microhabitat and structure-providing species, based on our field observations (e.g. *Serratula tinctoria*, *Sanguisorba officinalis* and *Genista tinctoria*). Due to several rare and specialist members (e.g. *Iris spuria*, *Centaurea scabiosa* subsp. *sadleriana* and *Ophrys* spp., etc.), native, annual and characteristic forbs are also important conservation targets. The occurrence and diversity of forbs in European steppe or forest-steppe grasslands have a long evolutionary history (Bråthen et al. 2020).

The increase of clonal, often highly competitive graminoid species with higher biomass production can reduce plant diversity (Deák et al. 2011; Házi et al. 2011; Szentes et al. 2012) and suppress conservation target species in grasslands (Kőrösi et al. 2014; Szépligeti et al. 2018), for example, several native forb species and their proportions (Figs 2–4). Therefore, the optimal and continuous control of clonal, competitive graminoids and the maintenance of optimal proportions of native and often specialist forbs is important in conservation practices for high nature value grasslands (Kun et al. 2021). This is most likely to be facilitated by high levels of management complexity and low levels of herbage removal intensity grazing (Figs 2–4). On the other hand, there was no significant difference between low and high levels of spatio-temporal complexity, herbage removal intensity or management type on graminoid cover, based on linear mixed model post hoc tests and, therefore, further studies are needed to analyse these relationships.

## Importance and challenges of studying the management complexity and other management factors in grassland conservation locally and across regions

Based on our results, special attention should be paid to the multiplicity of management factors (e.g. different management types or herbage removal intensity levels), including their spatio-temporal variability (Kun et al. 2021). We argue that taking these aspects into account can provide practitioners and stakeholders with more straightforward guidelines for conserving and restoring grassland diversity in the Turján Region. Local and regional scale case studies, as well as large-scale, comprehensive and comparative analyses of the effectiveness of different grass-

land conservation management techniques on different high nature value grassland communities in different regions, should be carried out in the future to gain more detailed and broader knowledge (see, for example, Fischer and Wipf (2002); Socher et al. (2012); Vadász et al. (2016); Kun et al. (2019); Rac et al. (2020)). This should provide a more complex view of the relationship between management practices and conservation objectives at the regional level, which could help to adapt grassland management to local conditions and challenges. Due to the often poor explanatory power of one-factor models, controversial management practices may arise in several cases (Babai et al. 2015; Kun et al. 2019), which may lead to locally ineffective conservation management (Vadász et al. 2016).

On the other hand, although we found that high management complexity is beneficial for grassland conservation, it may be difficult to apply such management complexity and the same methods in practice in other regions, for example, for several individual farmers. Our conclusions are most relevant in terms of the exact management complexity which we have investigated in our study. Each region is different in terms of management possibilities and environmental factors. It can be difficult to graze a site one year and mow it the next or to vary the intensity of management. It is also important to note that spatially and temporally complex management can be achieved in more ways than we have explored in our study. There are other and/or simpler ways, for example, mowing only every other year, mowing at the beginning of summer one year and at the end of summer the next. The use of different grazing animals and the leaving of uncut lines in different places on a grassland between years can also be effective tools for more complex management, depending on local conservation objectives and opportunities.

However, there are often practical difficulties in applying multiple aspects of management to the modelling of community diversity. Including more explanatory variables in a model requires larger sample sizes and a more balanced sample distribution (Harrison et al. 2018). Ideally, all possible factor combinations should be present in sufficient replicates without spatial autocorrelation across the study area. However, ongoing management plans are typically designed to meet different, often non-scientific, objectives and the actual management design rarely satisfies statistical assumptions. One can sample what is out there and if certain combinations of factors simply do not exist in reality, they will not be present in the statistical model. This increases multicollinearity in the models and makes it more difficult to distinguish the effects of different management factors (Graham 2003). This is a likely explanation for why the explanatory power of management type, intensity and complexity was similar in our models. Balanced sampling designs are relatively easier to achieve in experiments where factor levels and spatial structure can be varied to meet statistical requirements. On the other hand, more detailed assessments, based on multiple management factors in different parts and regions of Europe, would allow us to identify more comprehensively and accurately what should be included in conservation systems at larger scales, as well as in local practices.

## Implications

Our aim was to collect, organise and compare the elements of the hard-to-compare, mosaic-like landscape of use according to various parameters, using

systematic sampling and to quantify and generalise the treatment results obtained mainly through experience. We must emphasise as an important message to legislators and developers of support schemes that because each site is different, generalisation is limited.

High levels of management complexity and grazing as a management type are more positive and have a greater significance for grassland conservation (i.e. result in higher plant diversity, higher proportion of forbs etc.) than the intensity of herbage removal in our study area. At the same time, mowing and/or low levels of management complexity may have some negative effects on conservation value. These analyses can be used to identify what are the strong or direct and less strong or indirect effects in the conservation of high nature value grasslands. Further research is needed to verify these relationships across a wider range of different study systems in order to provide generalisable guidelines for conservation.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Data availability

All of the data that support the findings of this study are available in the main text.

## References

Allan E, Bossdorf O, Dormann CF, Prati D, Gossner MM, Tscharntke T, Blüthgen N, Bellach M, Birkhofer K, Boch S, Böhm S, Börschig C, Chatzinotas A, Christ S, Daniel R, Diekötter

T, Fischer C, Friedl T, Glaser K, Hallmann C, Hodac L, Hölzel N, Jung K, Klein AM, Klaus VH, Kleinebecker T, Krauss J, Lange M, Morris EK, Müller J, Nacke H, Pašalić E, Rillig MC, Rothenwöhrer C, Schall P, Scherber C, Schulze W, Socher SA, Steckel J, Steffan-Dewenter I, Türke M, Weiner CN, Werner M, Westphal C, Wolters V, Wubet T, Gockel S, Gorke M, Hemp A, Renner SC, Schöning I, Pfeiffer S, König-Ries B, Buscot F, Linsenmair KE, Schulze E-D, Weisser WW, Fischer M (2014) Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences of the United States of America 111(1): 308–313. https://doi.org/10.1073/pnas.1312213111

Babai D, Molnár Z (2014) Small-scale traditional management of highly species-rich grasslands in the Carpathians. Agriculture, Ecosystems & Environment 182: 123–130. https://doi.org/10.1016/j.agee.2013.08.018

Babai D, Tóth A, Szentirmai I, Biró M, Máté A, Demeter L, Szépligeti M, Varga A, Molnár Á, Kun R, Molnár Z (2015) Do conservation and agri-environmental regulations effectively support traditional small-scale farming in East-Central European cultural landscapes? Biodiversity and Conservation 24(13): 3305–3327. https://doi.org/10.1007/s10531-015-0971-z

Bakker JP, Berendse F (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution 14(2): 63–68. https://doi.org/10.1016/S0169-5347(98)01544-4

Box EO (1996) Plant functional types and climate at the global scale. Journal of Vegetation Science 7(3): 309–320. https://doi.org/10.2307/3236274

Bråthen K, Pugnaire FI, Bardgett R (2020) The paradox of forbs in grasslands and their legacy of the Mammoth steppe. Frontiers in Ecology and the Environment 19(10): 584–592. https://doi.org/10.1002/fee.2405

Catorci A, Cesaretti S, Malatesta L, Tardella FM (2014) Effects of grazing vs mowing on the functional diversity of sub-Mediterranean productive grasslands. Applied Vegetation Science 17(4): 658–669. https://doi.org/10.1111/avsc.12103

Dahlström A, Iuga AM, Lennartsson T (2013) Managing biodiversity rich hay meadows in the EU: A comparison of Swedish and Romanian grasslands. Environmental Conservation 40(2): 194–205. https://doi.org/10.1017/S0376892912000458

Deák B, Valkó O, Kelemen A, Török P, Miglécz T, Ölvedi T, Lengyel S, Tóthmérész B (2011) Litter and graminoid biomass accumulation suppresses weedy forbs in grassland restoration. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 145(3): 730–737.

Dumont B, Rossignol N, Loucougaray G, Carrère P, Chadoeuf J, Fleurance G, Bonis A, Farruggia A, Gaucherand S, Ginane C, Louault F, Marion B, Mesléard F, Yavercovski N (2012) When does grazing generate stable vegetation patterns in temperate pastures? Agriculture, Ecosystems & Environment 153: 50–56. https://doi.org/10.1016/j.agee.2012.03.003

Edwards LJ, Muller KE, Wolfinger RD, Qaqish BF, Schabenberger O (2008) An R2 statistic for fixed effects in the linear mixed model. Statistics in Medicine 27(29): 6137–6157. https://doi.org/10.1002/sim.3429

Erdélyi A, Hartdégen J, Malatinszky Á, Vadász C (2023) Historical reconstruction of the invasions of four non-native tree species at local scale: A detective work on *Ailanthus altissima*, *Celtis occidentalis*, *Prunus serotina* and *Acer negundo*. One Ecosystem 8: e108683. https://doi.org/10.3897/oneeco.8.e108683

Eriksson O, Cousins SA, Bruun HH (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science 13(5): 743–748. https://doi.org/10.1111/j.1654-1103.2002.tb02102.x

Fischer M, Wipf S (2002) Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. Biological Conservation 104(1): 1–11. https://doi.org/10.1016/S0006-3207(01)00149-5

Flynn DF, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12(1): 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84(11): 2809–2815. https://doi.org/10.1890/02-3114

Habel JC, Dengler J, Janišová M, Török P, Wellstein C, Wiezik M (2013) European grassland ecosystems: Threatened hotspots of biodiversity. Biodiversity and Conservation 22(10): 2131–2138. https://doi.org/10.1007/s10531-013-0537-x

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 23(6): e4794. https://doi.org/10.7717/peerj.4794

Házi J, Bartha S, Szentes S, Wichmann B, Penksza K (2011) Seminatural grassland management by mowing of *Calamagrostis epigejos* in Hungary. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 145(3): 699–707.

Hobohm C, Bruchmann I (2009) Endemische Gefäßpflanzen und ihre Habitate in Europa–Plädoyer für den Schutz der Grasland-Ökosysteme. Berichte der Reinhold-Tüxen-Gesellschaft 21: 142–161.

Hothorn T, Bretz F, Hothorn MT (2009) The Multcomp Package. The R Project for Statistical Computing.

Ives AR (2019) $R^2$s for Correlated Data: Phylogenetic Models, LMMs, and GLMMs. Systematic Biology 68(2): 234–251. https://doi.org/10.1093/sysbio/syy060

Kelemen A, Tölgyesi C, Kun R, Molnár Z, Vadász C, Tóth K (2017) Positive small-scale effects of shrubs on diversity and flowering in pastures. Tuexenia 37: 399–413.

Király G [Ed.] (2009) Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok. [New Hungarian Herbal. The vascular plants of Hungary. Identification key]. Aggteleki Nemzeti Park Igazgatóság, Jósvafő.

Knipl I, Sümegi P (2012) Life at the interface of two distinct landscapes-relationship of humans and environment in the periphery of the Danube-Tisza Interfluve between Hajós and Császártöltés. Open Geosciences 4(3): 439–447. https://doi.org/10.2478/s13533-011-0071-x

Kocsis K [Ed.] (2018) National Atlas of Hungary – Natural environment. Budapest, MTA CSFK Geographical Institute, 183 pp. https://www.nemzetiatlasz.hu/MNA/2_en.html

Kőrösi Á, Szentirmai I, Batáry P, Kövér S, Örvössy N, Peregovits L (2014) Effects of timing and frequency of mowing on the threatened scarce large blue butterfly–A fine-scale experiment. Agriculture, Ecosystems & Environment 196: 24–33. https://doi.org/10.1016/j.agee.2014.06.019

Krauss J, Klein AM, Steffan-Dewenter I, Tscharntke T (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. Biodiversity and Conservation 13(8): 1427–1439. https://doi.org/10.1023/B:BIOC.0000021323.18165.58

Kun R, Bartha S, Malatinszky Á, Molnár Z, Lengyel A, Babai D (2019) "Everyone does it a bit differently!": Evidence for a positive relationship between micro-scale land-use diversity and plant diversity in hay meadows. Agriculture, Ecosystems & Environment 283: e106556. https://doi.org/10.1016/j.agee.2019.05.015

Kun R, Babai D, Csathó AI, Vadász C, Kálmán N, Máté A, Malatinszky Á (2021) Simplicity or complexity? Important aspects of high nature value grassland management in nature conservation. Biodiversity and Conservation 30(12): 3563–3583. https://doi.org/10.1007/s10531-021-02262-z

Laliberte E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Morgan JW, Merlos DS, Vesk PA, Mayfield MM (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13(1): 76–86. https://doi.org/10.1111/j.1461-0248.2009.01403.x

MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Lazpita JG, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. Journal of Environmental Management 59(1): 47–69. https://doi.org/10.1006/jema.1999.0335

Marini L, Scotton M, Klimek S, Isselstein J, Pecile A (2007) Effects of local factors on plant species richness and composition of Alpine meadows. Agriculture, Ecosystems & Environment 119(3–4): 281–288. https://doi.org/10.1016/j.agee.2006.07.015

Mathar WP, Kämpf I, Kleinebecker T, Kuzmin I, Tolstikov A, Tupitsin S, Hölzel N (2016) Floristic diversity of meadow steppes in the Western Siberian Plain: Effects of abiotic site conditions, management and landscape structure. Biodiversity and Conservation 25(12): 2361–2379. https://doi.org/10.1007/s10531-015-1023-4

Maurer K, Weyand A, Fischer M, Stöcklin J (2006) Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. Biological Conservation 130(3): 438–446. https://doi.org/10.1016/j.biocon.2006.01.005

Molnár Z, Kelemen A, Kun R, Máté J, Sáfián L, Provenza F, Díaz S, Barani H, Biró M, Máté A, Vadász C (2020) Knowledge co-production with traditional herders on cattle grazing behaviour for better management of species-rich grasslands. Journal of Applied Ecology 57(9): 1677–1687. https://doi.org/10.1111/1365-2664.13664

Molnár ÁP, Erdélyi A, Hartdégen J, Biró M, Pánya I, Vadász C (2022) Historical analysis for nature conservation – the past three centuries of the Peszér forest. Journal of Landscape Ecology 20(1): 73–105. https://doi.org/10.56617/tl.3381

Niedrist G, Tasser E, Lüth C, Dalla Via J, Tappeiner U (2009) Plant diversity declines with recent land use changes in European Alps. Plant Ecology 202(2): 195–210. https://doi.org/10.1007/s11258-008-9487-x

Öckinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149(3): 526–534. https://doi.org/10.1007/s00442-006-0464-6

Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological Conservation 133(3): 291–300. https://doi.org/10.1016/j.biocon.2006.06.009

Plieninger T, Höchtl F, Spek T (2006) Traditional land-use and nature conservation in European rural landscapes. Environmental Science & Policy 9(4): 317–321. https://doi.org/10.1016/j.envsci.2006.03.001

Poschlod P, Kiefer S, Tränkle U, Fischer S, Bonn S (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. Applied Vegetation Science 1(1): 75–91. https://doi.org/10.2307/1479087

R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Rac I, Juvančič L, Erjavec E (2020) Stimulating collective action to preserve High Nature Value farming in post-transitional settings. A comparative analysis of three

Slovenian social-ecological systems. Nature Conservation 39: 87–111. https://doi.org/10.3897/natureconservation.39.51216

Raunkiær C (1934) The Life Forms of Plants and Statistical Plant Geography; Being the Collected Papers of C. Raunkiær.

Schneiders A, Van Daele T, Van Landuyt W, Van Reeth W (2012) Biodiversity and ecosystem services: Complementary approaches for ecosystem management? Ecological Indicators 21: 123–133. https://doi.org/10.1016/j.ecolind.2011.06.021

Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology 100(6): 1391–1399. https://doi.org/10.1111/j.1365-2745.2012.02020.x

Szentes S, Sutyinszki Z, Szabó G, Zimmermann Z, Házi J, Wichmann B, Hufnágel L, Penksza K, Bartha S (2012) Grazed Pannonian grassland beta-diversity changes due to C 4 yellow bluestem. Open Life Sciences 7(6): 1055–1065. https://doi.org/10.2478/s11535-012-0101-9

Szépligeti M, Kőrösi Á, Szentirmai I, Házi J, Bartha D, Bartha S (2018) Evaluating alternative mowing regimes for conservation management of Central European mesic hay meadows: a field experiment. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 152(1): 90–97. https://doi.org/10.1080/11263504.2016.1255268

Tälle M, Deák B, Poschlod P, Valkó O, Westerberg L, Milberg P (2016) Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. Agriculture, Ecosystems & Environment 222: 200–212. https://doi.org/10.1016/j.agee.2016.02.008

Tölgyesi C, Torma A, Bátori Z, Seat J, Popovic M, Gallé R, Gallé-Szpisjak N, Erdős L, Vinkó T, Kelemen A, Török P (2022) Turning old foes into new allies – harnessing drainage canals for biodiversity conservation in desiccated novel ecosystems. Journal of Applied Ecology 59: 89–102. https://doi.org/10.1111/1365-2664.14030

Török P, Penksza K, Tóth E, Kelemen A, Sonkoly J, Tóthmérész B (2018) Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. Ecology and Evolution 8(20): 10326–10335. https://doi.org/10.1002/ece3.4508

Vadász C, Máté A, Kun R, Vadász-Besnyői V (2016) Quantifying the diversifying potential of conservation management systems: An evidence-based conceptual model for managing species-rich grasslands. Agriculture, Ecosystems & Environment 234: 134–141. https://doi.org/10.1016/j.agee.2016.03.044

von Glasenapp M, Thornton TF (2011) Traditional ecological knowledge of Swiss alpine farmers and their resilience to socioecological change. Human Ecology: an Interdisciplinary Journal 39(6): 769–781. https://doi.org/10.1007/s10745-011-9427-6

Willner W, Rolecek J, Korolyuk A, Dengler J, Chytry M, Janisova M, Lengyel A, Aćić S, Becker T, Cuk M, Demina O, Jandt U, Kącki Z, Kuzemko A, Kropf M, Lebedeva M, Semenishchenkov Y, Šilc U, Stančić Z, Staudinger M, Vassilev K, Yamalov S (2019) Formalized classification of semi-dry grasslands in central and eastern Europe. Preslia 91(1): 25–49. https://doi.org/10.23855/preslia.2019.025

## Appendix 1

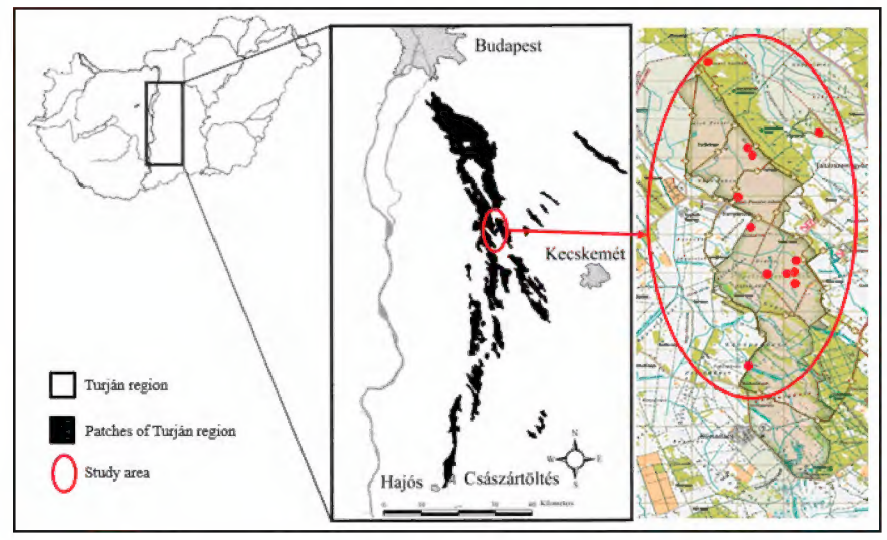


**Figure A1.** Study area and location of the twelve sampled meso-xeric grassland sites (Knipl and Sümegi 2012).

## Appendix 2

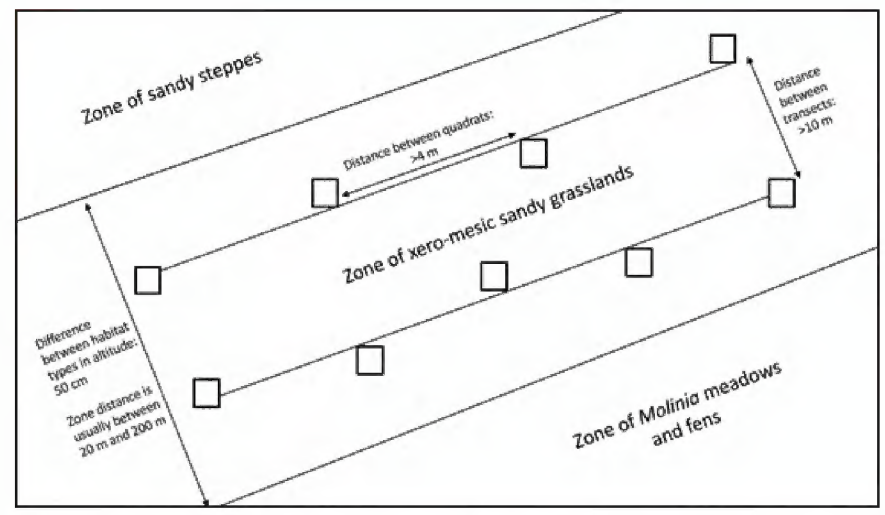
Zone of sandy steppes
Distance between quadrats: >4 m
Distance between transects: >10 m
Zone of xero-mesic sandy grasslands
Difference between habitat types in altitude: 50 cm
Zone distance is usually between 20 m and 200 m
Zone of Molinia meadows and fens

**Figure A2.** Distances between an elevation of Molinia meadows and fens and a sandy steppe zone. For the field sampling, nine plots were established along two transects in each grassland site. The distance between two transects was at least 10 m and the distance between the quadrats was at least 4 m.

## Appendix 3

**Table A1.** Sampling design in the study area with factor combinations at each site and number of replicates.

| Number of sites | Management type | Herbage removal intensity | Management complexity | Number of management factor combinations | Number of plots per site |
|---|---|---|---|---|---|
| 1 | Mown | Low | Low | 1 | 9 |
| 2 | Mown | Low | Low | 1 | 9 |
| 3 | Mown | Low | Low | 1 | 9 |
| 4 | Grazed | Low | High | 2 | 9 |
| 5 | Grazed | Low | High | 2 | 9 |
| 6 | Grazed | High | Low | 3 | 9 |
| 7 | Grazed | High | Low | 3 | 9 |
| 8 | Grazed | High | Low | 3 | 9 |
| 9 | Grazed | High | High | 4 | 9 |
| 10 | Combined | Low | Low | 5 | 9 |
| 11 | Combined | Low | High | 6 | 9 |
| 12 | Combined | High | High | 7 | 9 |

## Appendix 4

**Table A2.** Differences in PFT cover and diversity indices between different management types (mowing: *M*, grazing: *G* and combined: *C*) of semi-natural grasslands. The Table shows means and standard deviations of PFT groups and diversity indices. Significant differences in LMER Tukey post hoc tests between different management types are indicated by the letters 'a', 'b' and 'c'.

| | ***MOWN*** | ***GRAZED*** | ***COMBINED*** |
|---|---|---|---|
| Species number | 34.1±3.2a | 34.9±5.8a | 35.4±3.5a |
| Shannon diversity | 1.6±0.4a | 1.9±0.3b | 1.8±0.3b |
| Simpson diversity | 0.6±0.2a | 0.7±0.1b | 0.7±0.1b |
| Forbs cover (%) | 19.0±11.9a | 24.4±15.2a | 31.1±20.2a |
| Graminoid cover (%) | 82.2±11.3a | 74.3±18.2a | 57.8±22.2a |
| Phanerophytes cover (%) | 2.2±1.7a | 5.1±3.8b | 4.0±4.0ab |
| Mean plant height (cm) | 31.4±12.8a | 26.7±8.4a | 21.0±8.4a |
| Total plant cover (%) | 94.0±3.3a | 95.6±3.1a | 87.6±8.7a |
| Bare soil surface (%) | 0.6±0.4a | 1.6±1.6a | 1.8±1.9a |
| Litter cover (%) | 5.7±3.3a | 3.8±2.7a | 10.9±7.7a |

## Appendix 5

**Table A3.** Effects of herbage removal intensity of management on plant diversity and cover of PFTs. Table shows means and standard deviations of PFT cover and diversity indices. Results are based on LMER Tukey post hoc tests. Significant differences between different intensity levels are indicated by the letters 'a' and 'b'.

| | ***LOW*** | ***HIGH*** |
|---|---|---|
| Species number | 34.3±4.7a | 35.6±4.6a |
| Shannon diversity | 1.7±0.4a | 1.8±0.4a |
| Simpson diversity | 0.7±0.1a | 0.7±0.1a |
| Forbs cover (%) | 26.4±19.1a | 22.5±11.3a |
| Graminoid cover (%) | 66.9±21.3a | 79.5±15.1a |
| Phanerophytes cover (%) | 4.4±3.9a | 3.7±3.3a |
| Mean plant height (cm) | 25.9±10.8a | 26.5±9.2a |
| Total plant cover (%) | 91.3±6.8a | 96.0±3.3a |
| Bare soil surface (%) | 1.3±1.7a | 1.6±1.6a |
| Litter cover (%) | 8.0±5.9a | 3.2±2.4a |

## Appendix 6

**Table A4.** Differences between two levels of management complexity (low and high) on plant diversity and plant functional types. Table shows means and standard deviations of PFT cover and diversity indices. Results are based on LMER Tukey post hoc tests. Significant differences between different levels of management complexity are indicated by the letters 'a' and 'b'.

| | ***LOW*** | ***HIGH*** |
|---|---|---|
| Species number | 35.0±3.8a | 34.6±5.8a |
| Shannon diversity | 1.7±0.4a | 1.9±0.4b |
| Simpson diversity | 0.6±0.1a | 0.7±0.1b |
| Forbs cover (%) | 24.2±17.2a | 25.6±15.3a |
| Graminoid cover (%) | 76.3±21.2a | 66.3±16.2a |
| Phanerophytes cover (%) | 3.4±2.9a | 5.2±4.3a |
| Mean plant height (cm) | 29.7±10.2a | 22.2±8.6a |
| Total plant cover (%) | 94.4±4.5a | 91.5±7.5a |
| Bare soil surface (%) | 1.0±0.9a | 1.8±2.0a |
| Litter cover (%) | 5.2±3.9a | 7.3±6.8a |

## Appendix 7

**Table A5.** Differences in species composition dissimilarity between management types and levels of herbage removal intensity and management complexity, based on PERMANOVA analyses and Jaccard dissimilarity index.

| | **Df** | **Sums of Sqs** | **Mean Sqs** | **F-test** | **$R^2$** | **Pr(> F)** |
|---|---|---|---|---|---|---|
| ***T*** | 2 | 3.126 | 1.563 | 5.792 | 0.099 | 0.001 *** |
| Residuals | 105 | 28.332 | 0.270 | | 0.901 | |
| Total | 107 | 31.458 | | | 1.000 | |
| ***I*** | 1 | 0.980 | 0.980 | 3.409 | 0.031 | 0.001 *** |
| Residuals | 106 | 30.478 | 0.288 | | 0.969 | |
| Total | 107 | 31.458 | | | 1.000 | |
| ***C*** | 1 | 1.783 | 1.783 | 6.368 | 0.057 | 0.001 *** |
| Residuals | 106 | 29.675 | 0.280 | | 0.943 | |
| Total | 107 | 31.458 | | | 1.000 | |

## Appendix 8

**Table A6.** Proportion of principal components expressed by eigenvalues, explained and cumulative proportions and their contribution to the variance.

| | **PC1** | **PC2** | **PC3** | **PC4** | **PC5** | **PC6** | **PC7** |
|---|---|---|---|---|---|---|---|
| Eigenvalue | 724.490 | 179.844 | 50.093 | 14.880 | 7.097 | 2.952 | 0.420 |
| Explained share | 0.739 | 0.184 | 0.051 | 0.015 | 0.007 | 0.003 | 0.000 |
| Cumulative share | 0.739 | 0.923 | 0.974 | 0.989 | 0.997 | 0.100 | 1.000 |